IOLOGY OF THE SEA LAMPREY
N ITS PARASITIC PHASE

RESEARCH REPORT 44

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ABSTRACT

The investigations conducted on sea lampreys in aquariums were concerned with the duration of the parasitic phase of life, feeding, growth, and the interrelations between predator and host fish. Observations on lampreys reared from metamorphosis to maturity were made at the Fish and Wildlife Service Laboratory at Hammond Bay, Mich.

Most of the experimental lampreys were mature and ripe after 14 to 18 months of parasitic life. They exhibited signs of irreversible physical degeneration which precedes death. Three specimens were immature after 14, 18, and 26 months in aquariums, thus indicating that under certain conditions, lampreys may extend their parasitic phase.

The feeding activity, growth, and shrinkage in size of aquarium specimens were considered typical of lampreys in the Great Lakes, although the wild lampreys achieve greater average size. Female lampreys made more attacks, fed more, killed more fish, and grew larger than males. They also shrank proportionately more in length and weight as they approached sexual maturity, but their terminal average size was slightly larger than that of males.

It is estimated that the average fish-kill by a wild lamprey exceeds, and could be approximately double, the 18.5 pounds of fish killed by a laboratory lamprey. The rate and extent of fish destruction depended on the size, sex, and stage in the parasitic phase of the lampreys, and on the species and size of the fish. There was an increase in the number of fish killed as the lampreys grew, and the fish were killed more quickly. Attacks made by experimental lampreys at any stage of their parasitic phase up to full maturity, and on any part of a prey fish except fins, usually resulted in death to the host.

Some fish which survived lamprey attacks succumbed to fungus infections of the wounds. A small number of trout recovered from attacks, and their wounds healed.

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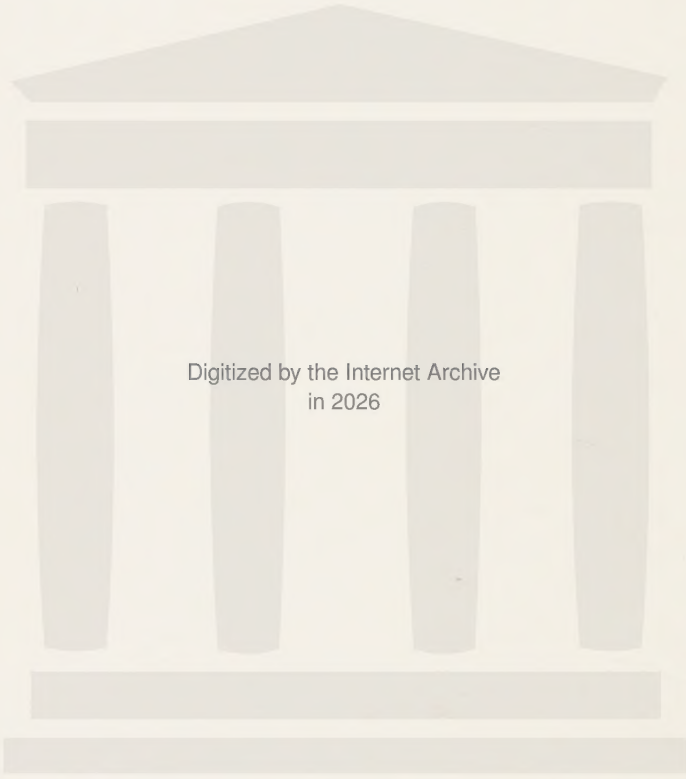
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BIOLOGY OF THE SEA LAMPREY IN ITS PARASITIC PHASE

Comprehensive investigations on the sea lamprey in the Great Lakes were inaugurated by the Fish and Wildlife Service in 1949. The objective of the program is the suppression or control of this predatory parasite, which has so severely damaged the fisheries of Lakes Huron and Michigan and presently threatens those of Lake Superior.

Early information on the invasion of the lakes by sea lampreys and the possible consequences thereof were reported by Creaser (1932), Hubbs and Pope, (1937), Applegate (1947), Shetter (1949), and others. The present investigations have produced important findings on the natural history of the sea lampreys in the lakes (Applegate 1950), on their distribution and spawning migrations (Applegate and others 1952; Loeb and Hall, 1952; and Loeb 1953), on their movements in the lakes (Smith and Elliott, 1953), on their diseases and parasites (McLain 1952), on their feeding mechanism and its deadly effects on fish (Lennon 1954), and the consequences of their predation on commercial fisheries (Hile 1949; Hile, Eschmeyer, and Lunger, 1951; and Hall and Elliott, 1954). Promising methods of control of sea lampreys were reported by Applegate, Smith, and Nielson, (1952); and Applegate and Moffett (1955).

Certain aspects in the life history of sea lampreys required further investigation and elaboration because of their significance in devising a practical control program and in evaluating the damage wrought by lampreys on the commercial and sport fisheries. Aquarium facilities were provided at the Hammond Bay Fishery Laboratory for study of the duration of the parasitic phase, of feeding and growth, of interrelation of lampreys and prey fish, and of the quantity of fish destroyed by the average lamprey. Observations on captive lampreys in the aquariums were begun in June 1950 on a limited scale. The facilities were improved and the program expanded in November 1950. The study continued until June 1952.

Albert E. Hall, Jr., Clifford L. Brynildson, and Allen C. Bennett assisted in maintaining records and processing specimens; their contributions of time and effort enabled us to extend observations over many nights, weekends, and holidays. Oliver R. Elliott and Vern Seaman were especially helpful in providing adequate numbers of live fish for use in the aquariums. Also we wish to acknowledge the aid extended to us by other members of the Great Lakes Fishery Investigations.

FACILITIES AND METHODS

Aquariums and tanks

Facilities at the Hammond Bay Fishery Laboratory for the experimental study of sea lampreys included twelve 50-gallon aquariums furnished with running water from Lake Huron. Compressed air was supplied for aeration in the event of failure of the water supply. The aquarium system proved suitable for holding sea lampreys and fish for long periods of time.

Water pumped from the lake was usually clear and colorless, free of organic material, saturated with dissolved oxygen, and relatively free of dissolved carbon dioxide (table 1). Storms and heavy surf in the lake caused turbid conditions in the aquariums at times. Brief periods of extreme turbidity interrupted feeding by the lampreys and caused some mortality among lampreys and fish.

Water temperatures in the lake and in the aquariums were continually recorded on thermographs. Since the intake lines of the water supply were located near the shore in Hammond Bay, the range of water temperatures in the aquariums exceeded that in the deeper waters of the bay. It was determined through experimentation, however, that the temperatures in the aquariums were well within the range of tolerance for sea lampreys and the prey fish.

Additional facilities for holding fish to be used as prey for the lampreys consisted of large livecars in Hammond Bay and large concrete and steel tanks in the laboratory. The tanks were supplied with running water from the lake. It was possible to maintain several hundred fish on hand during periods of ice cover or inclement weather when fresh specimens would otherwise be unobtainable.

Table 1.—Selected data on water pumped from Lake Huron to aquariums and tanks in which sea lampreys and fish were held

[Readings for aquariums 1 and 10 and concrete tank A were representative of other aquariums and tanks]

Date and aquarium or tank	Water temperature (° F.)	pH	Dissolved oxygen (p. p. m.)	Dissolved carbon dioxide (p. p. m.)
1951				
July 11–12:				
Aquarium 1	61.5	-----	8.2	2.0
Aquarium 10	61.5	7.8	8.6	3.0
Tank A	61.5	-----	7.2	4.0
Aug. 27:				
Aquarium 1	63.0	-----	8.4	-----
Aquarium 10	63.0	-----	9.4	-----
Tank A	63.0	-----	7.0	-----
Sept. 13:				
Aquarium 1	63.5	7.8	8.4	3.0
Aquarium 10	63.5	7.8	8.6	3.0
Tank A	63.5	7.6	8.2	3.0
Sept. 26–27:				
Aquarium 1	54.0	7.8	10.6	3.0
Aquarium 10	54.0	7.8	10.8	3.0
Oct. 17:				
Aquarium 1	53.0	7.6	7.2	2.0
Aquarium 10	53.0	7.6	9.7	2.0
Nov. 21:				
Aquarium 1	35.0	7.7	13.3	3.0
Aquarium 10	35.0	7.7	13.3	3.0
Dec. 18:				
Aquarium 1	34.0	7.9	14.3	2.0
Aquarium 10	34.0	7.8	14.3	2.0
1952				
Jan. 25:				
Aquarium 1	34.0	7.8	11.7	2.0
Aquarium 10	34.0	7.8	12.2	2.0
Tank A	34.0	-----	11.4	2.5
Jan. 29:				
Aquarium 1	34.0	-----	14.2	-----
Aquarium 10	34.0	-----	14.2	-----
Feb. 27:				
Aquarium 1	34.5	7.6	12.3	1.8
Aquarium 10	34.5	7.6	12.8	1.8
Mar. 26:				
Aquarium 1	35.0	7.7	12.7	2.0
Aquarium 10	35.0	7.7	13.0	2.0
Apr. 17:				
Aquarium 1	36.0	7.5	11.1	2.0
Aquarium 10	36.0	7.5	11.0	2.0
May 22:				
Aquarium 1	55.0	8.0	9.3	2.0
Aquarium 10	55.0	8.0	9.0	2.0

The specimens

Lampreys.—The sea lampreys stocked in the aquariums had completed their larval life and had

ecently transformed into the parasitic form capable of feeding on fish. They were captured in an inclined-plane trap in Carp Lake River, Emmett County, Mich., during their downstream, lakeward migration. Two groups of spring migrants (April 1950 and May 1951) and one group of fall migrants (November 1950) were used. Some observations were obtained on lampreys which had spent a portion of their parasitic life in Lake Huron before they were captured in trap nets and transferred to aquariums.

The number of lampreys in the experimental series was limited by the available aquariums and to some extent by early limitations in water supply. It was necessary to exercise constant precautions to keep the specimens healthy. They appeared to be particularly susceptible to fungus infections which frequently started in minor injuries and abrasions received while attached to wildly struggling fish. Outbreaks of *Saprolegnia* sp. were arrested by constant-flow applications of malachite-green solution (1:15,000). Some infections by *Leptomitus* sp. were encountered, but no effective remedies were found.

An interruption in the experiment occurred between July 21 and August 1, 1951, because many lampreys had become infested by a protozoan parasite (*Ichthyophthirius* sp.) and several died. The lampreys were removed from the aquariums and transferred for 2 weeks to shallow troughs containing rapidly flowing water, and the infestation disappeared.

Fish.—Among the species of fish used in the aquariums were small numbers of brown trout (*Salmo trutta*) and eastern brook trout (*Salvelinus fontinalis*) captured in nearby streams; yearling rainbow trout (*Salmo gairdneri*) and lake trout (*Salvelinus namaycush*) contributed by the Michigan Department of Conservation from the Oden fish hatchery; and white suckers (*Catostomus c. commersoni*), longnose suckers (*C. c. catostomus*), and yellow perch (*Perca flavescens*) captured in our trap nets in Duncan and Hammond Bays of Lake Huron. It appeared desirable to use the commercially important lake trout and whitefish (*Coregonus clupeaformis*) as prey for the experimental lampreys, but these species had been wiped out or made extremely scarce by lampreys in nearby areas of former abundance and were unavailable to us. The wild white suckers and the hatchery-reared rainbow trout were the principal species used throughout the study, and they may be considered, in a general way at least, to be representative of other trouts and of coregonids (Lennon 1954).

Trout were maintained in good condition in the aquariums and holding tanks for periods ranging from a day to several months before they were attacked and killed by lampreys. They were fed with a hatchery-type diet; occasionally small cyprinids and chopped fish were also used. Aside from the intent to keep the trout in good condition, it had been assumed that unless they were fed, the larger brown, rainbow, and brook trout (10 to 13 inches long) might prey on the newly transformed lampreys

(5 to 7 inches long). Although the trout attacked and attempted to swallow the small lampreys, they invariably spat them out quickly, forcefully, and unharmed, as though the lampreys were very distasteful. It was determined that trout which had been starved for 1 to 2 weeks would still grasp, but soon release, small lampreys. When mixtures of diced lamprey flesh and sucker flesh were offered, the sucker material was eaten by the trout, but pieces of lamprey flesh were quickly discarded. No losses of lampreys occurred from predation by the wild and hatchery-reared trout.

The records

Each lamprey and fish used in the aquariums was given a specimen number and a readily distinguishable fin clip, and individual data sheets were maintained. A record was made for each lamprey on the initiation, duration, and termination of its attacks on fish, on the hours of feeding and nonfeedi attachment, on whether or not t host died, and on the identiti and sizes of the hosts. Periodi ally the lampreys were remov from the aquariums, anesthetiz in urethane (4-percent solutio measured, and weighed.

For each prey fish, we record the species, its size, its source, t date and hour of its entry into aquarium, dates and hours of a tacks and detachments by la preys, the identity of each attack the locations of feeding and no feeding attachments on its bod its reactions to attacks, and t time of death. Small sketches we provided on the record sheets that the locations of attacks on t body of the fish could be accurate and easily plotted. Each fish w examined upon its death and moval from the aquarium, and data sheet was checked before was filed.

DURATION OF PARASITIC PHASE

Knowledge of the life span of sea lampreys in the Great Lakes is a matter of extreme importance in the consideration of measures for control of the parasite. Applegate (1950) estimated that adult lampreys spend between 12 and 20 months in the lakes. The estimate was based on analyses of the size composition of specimens collected in the lakes and during downstream and upstream migrations. The studies on sea lampreys in aquariums at the Hammond Bay Fishery Laboratory have provided additional information on average and range in duration of parasitic life.

First experimental series

The 2-year program of inves gation on the life span, grow rate, and feeding habits of adu sea lampreys was initiated in Ap 1950. At that time approximate 350 newly transformed lampre were captured during their lakewa migration in Carp Lake River a held in livecars until June, wh they were transferred to aquariu and furnished with prey fish.

Serious difficulties were imm diately encountered in maintai ing suitable water conditions in t aquariums, and most of the la preys in the experimental ser

lied within 2 months. No or-anized records on feeding, nd survival were maintained on his series of lampreys before No-ember 1950. There were only 10 urvivors in June 1951, of which 9 vere killed and reported to be exually mature. They exhibited econdary sex characters and signs f degeneration which attend pawning and death (Applegate 950). The remaining specimen, dentified hereafter as CL–10, con-inued feeding; it appeared to be mmature and was spared for fur-her observation.

Hall and Parker (1951) [1] reported n this series of lampreys stocked n aquariums. Among their con-lusions regarding the 9 specimens vhich survived until June 1951 were he following: Parasitic-phase speci-nens lived, fed, and reached matu-ity in aquariums; their maturation vas accompanied by physiological egeneration; and only 1 spawning eriod was possible for any mature pecimen.

econd experimental series

Comprehensive observations on a econd series of experimental sea ampreys were begun in November 950. A part of this series included 0 downstream migrants taken from arp Lake River at the peak of the utumn, lakeward movement (table). This group was transferred im-ediately to aquariums on Novem-er 22. Their average length was 7 inches (range, 5.1 to 7.1 inches) nd average weight was 4 grams (range, 2 to 8 grams). Each specimen was marked by clipping all or a portion of one or more fins, and an identity number was assigned. Small brook trout, 5 to 9 inches long, were marked and placed in the aquariums as prey. At a later date, wild brown trout, hatchery-reared rainbow trout, and white suckers from Lake Huron were also used as host fish.

The remainder of the second series of experimental lampreys included 60 newly transformed specimens taken at the peak of the spring, downstream migration and immediately placed in aquariums on May 3, 1951 (table 2). According to Applegate (1950), these specimens belonged to the same year class of lampreys as the 40 individuals described above. Their average length was 5.5 inches (range, 4.8 to 6.6 inches) and average weight was 3.6 grams (range, 2 to 6 grams).

Table 2.—Number and percentage of survival of lampreys in aquariums, second experimental series, November 1950 and May 1951

Measuring period	November group		May group	
	Number	Percentage of survival	Number	Percentage of survival
1950				
Nov. 22	40	100.0	----------	--------
1951				
May 3	36	90.0	60	100.0
July 2	25	62.5	52	86.7
Aug. 13	17	42.5	40	66.7
Sept. 24	7	17.5	26	43.3
Nov. 5	7	17.5	24	40.0
Dec. 17	6	15.0	23	38.3
1952				
Feb. 4	6	15.0	21	35.0
Mar. 17	6	15.0	19	31.7
May 20	6	15.0	16	26.7
June 26	6	15.0	16	26.7
Total term survivors	6	15.0	16	26.7

[1] Aquarium studies on the parasitic phase of the life cle of the sea lamprey, by A. E. Hall, Jr., and Phillip Parker. Great Lakes Fishery Investigations, U. S. sh and Wildlife Service. Mimeographed progress ort, 15 pp.

Before June, there were as many as 20 lampreys in each 50-gallon aquarium; as more tanks became available, the specimens were redistributed at 10 per tank. There was considerable mortality among the experimental lampreys from fungi, parasitic protozoa, turbidity, and other undetermined causes, and the number of lampreys per tank was further reduced to 2 to 4 individuals. Between early May and late September, 72.5 percent of the 40 November specimens and 46 percent of the 60 May specimens died. Only 6 lampreys (15 percent) of the fall group and 16 (26.7 percent) of the spring group survived the full term of the experiment. Throughout this report these 22 survivors are frequently referred to as "term" lampreys. A serious breakdown of aquarium facilities forced the conclusion of observations in June 1952. Thereby we lost a valuable opportunit to obtain positive information c the length of parasitic life aquariums, to observe the fu process of maturation to ripenes and to determine the extent physical degeneration precedi death.

The term lampreys were kill and examined on June 25 and 2 The sudden end of the experime compelled us to resort to arbitra criteria in evaluating maturity ar the progress of degeneration each specimen. The indexes us in estimating the extent of matur tion were those noted by Applega (1950) in ripe sea lampreys ca tured during upstream migrati or over spawning grounds (table 3 They include such morphologic and physiological manifestations deterioration of eyes and epidermi change in skin color, developme of dorsal ridges on males and ve

Table 3.—Criteria employed in evaluation of maturity in experimental sea lampreys

[Characters for immaturity were derived from observations on specimens from laboratory and lake sources; ch acters for sexually mature lampreys taken from Applegate (1950) and from spawning migrants dissected the laboratory]

Character	Immature lampreys	Sexually mature lampreys	Immature term lampreys		
			Specimen CL-10	Specimen CL-28	Specime CL-85
Epidermis	Normal	Degenerate	Normal	Normal	Normal.
Condition of eyes	do	do	do	do	Do.
Color of skin	Black and white	Yellow-brown	Black and white.	Black and white.	Black a white.
Secondary sex characters:					
Males	Negative	Dorsal ridge	Negative	Negative	Negative
Females	do	Ventral keel	do	do	Do.
Color of liver	Pale red-orange	Green	Pale orange.	Pale orange.	Pale oran
Mean diameter of intestine, millimeters.	9.1 [1] 9.5 [2]	2.3	6.0	7.5	6.7.
Range	8.3–10.3 7.8–11.2	1.5–3.0	4.0–9.0	5.0–10.0	4.4–7.7.
Weight of ovary expressed as percentage of total body weight.	1.6 [3]	22.4	4.5	4.9	
Range	0.9–2.9	13.6–29.5			
Mean diameter of ova, millimeters	0.4	1.10	0.3	0.5	
Range	0.3–0.5	0.8–1.3		0.4–0.6	
Weight of testes as percentage of total body weight.	1.0	2.2			1.2.
Range	0.2–2.0	1.1–3.5			

[1] Determined from selected specimens which ranged from 13.0 to 13.9 inches long.
[2] Determined from selected specimens which ranged from 14.0 to 14.9 inches long.
[3] Based on 5 immature females which died after 4 to 7 months of adult life.

tral keels on females, atrophy of intestine, discoloration of liver, and relative increase in size of gonads. The degenerative process in a mature lamprey is irreversible, and death soon follows whether or not spawning takes place.

November group.—Of the 6 survivors of the November 1950 group of lampreys, 5 were sexually mature and ripe, or nearly so, after 18 months of adult life in aquariums (table 4). They exhibited the sex characters and the signs of physical degeneration which accompany maturity.

The exception in the group was lamprey CL–28. She showed no change in the color of her body and the condition of her eyes, there were no secondary sex characters, and her liver was dull orange instead of green. The average diameter of eggs was 0.528 millimeter as compared with the mean of 1.10 millimeters listed by Applegate (1950) for fully developed eggs; the weight of the ovaries, expressed as percentage of total body weight, was 4.9, or about one-quarter that given for mature females; and the mean diameter of the intestine was 7.5 millimeters as compared with an average of 2.3 millimeters in atrophied intestines. Consequently, CL–28 was considered immature. There is little evidence that she would have become ripe during the 1952 spawning season (May through August).

May group.—The 16 survivors of the May 1951 group of 60 experimental lampreys showed various degrees of maturity when they were killed on June 25 and 26, 1952, after nearly 14 months of parasitic life in aquariums. Twelve lampreys were sexually mature and ripe, or nearly so. Specimens CL–78, CL–107, and CL–113 were mature but their gonads had not attained maximum development. They might have ripened within a few weeks. Specimen CL–85 was immature and its eyes, skin, liver, intestine, and testes were similar in condition to those of known immature sea lampreys (table 4). He was still growing, and his last feeding attack on a fish took place just 12 days before the conclusion of the experiment.

Specimen CL–10.—Lamprey CL–10, the specimen that carried over from the previous year class, failed to show any signs of maturity during its second year of parasitic life in aquariums. At the beginning of its third summer, the experiment was discontinued, and CL–10 was killed and examined on June 26, 1952, 26 months after its capture as a downstream migrant in Carp Lake River. It was a female and still immature. No changes were noted in the condition of eyes and skin; little or no degeneration of the intestine had occurred; the liver was pale orange; and the weight of the ovaries and size of the eggs were small (table 3). We cannot say whether CL–10 would have become sexually mature before the end of the 1952 spawning season. The fact remains however that it spent an additional year as an actively feeding parasite after other lampreys of the same experimental series had matured.

It was concluded that most sea lampreys held in aquariums would spend between 13 and 18 months as parasitic feeders before maturing

and dying. There is a possibility that specimens CL–10, CL–28, and CL–85 failed to mature as a result of unknown, adverse conditions in the laboratory and that such tardiness may not be common in the lakes. It is significant, however, that lampreys can extend parasitic life under certain conditions; hence, exceptions to Applegate's (1950) estimate of parasitic life span might occur in the Great Lakes. It is unfortunate that collection of conclusive evidence concerning the duration of the parasitic phase in aquarium specimens was prohibited by premature termination of the experiment.

Table 4.—Size, sex, and degree of maturity of sea lampreys of the second experimental series which survived in aquariums until the termination of the parasitic-phase study

[Downstream migrants were stocked in aquariums in November 1950 and May 1951. Survivors of both groups were killed in June 1952]

Specimen number	Initial size		Maximum size		Terminal size		Sex	Degree of maturity
	Length (inches)	Weight (grams)	Length (inches)	Weight (grams)	Length (inches)	Weight (grams)		
November migrants:								
CL–25	5.5	4	15.2	90	12.5	48	M	Ripe.
CL–28	5.8	4	13.5	54	12.5	40	F	Immature.
CL–34	5.9	4	15.0	84	12.8	57	F	Ripe.
CL–37	5.7	4	16.0	119	13.6	69	M	Do.
CL–38	5.6	4	15.2	86	13.3	52	M	Do.
CL–43	5.5	4	16.5	112	13.3	59	F	Do.
May migrants:								
CL–78	5.7	4	12.7	50	10.2	35	M	Unripe.
CL–85	5.1	3	13.4	55	13.4	55	M	Immature.
CL–86	4.9	2	14.6	92	12.1	49	F	Ripe.
CL–88	6.2	5	15.7	88	13.0	54	M	Do.
CL–91	5.5	3	13.4	60	12.0	42	M	Do.
CL–94	4.9	3	14.5	74	12.6	47	F	Do.
CL–95	5.5	4	14.1	63	12.5	50	M	Do.
CL–97	5.1	2	15.0	84	13.0	55	M	Do.
CL–98	5.9	4	16.1	135	14.3	104	M	Do.
CL–107	6.4	6	14.7	70	12.6	38	F	Unripe.
CL–108	5.5	3	12.9	62	11.7	50	M	Ripe.
CL–113	5.1	2	14.1	72	11.7	36	M	Unripe.
CL–115	6.0	4	15.1	84	12.7	40	M	Ripe.
CL–116	5.0	2	15.5	98	13.1	55	M	Do.
CL–121	5.2	2	13.2	52	10.6	32	M	Do.
CL–127	5.7	3	17.4	129	14.3	80	F	Do.

FEEDING AND GROWTH OF ADULT SEA LAMPREYS

The feeding mechanism of parasitic-phase sea lampreys is adapted for obtaining liquid food. Blood, body juices, and liquefied flesh of fish are ingested by lampreys in their attacks (Lennon 1954). Little was known, however, about the amount of feeding required to carry newly transformed sea lampreys through the parasitic phase to maturity, and about their rate of growth through this phase. Information on these points was obtained from the specimens held in aquariums. The relations among feeding, growth, season, and maturity were studied.

Feeding and growth data were collected from the newly transformed lampreys of the second experimental series which were marked and placed in aquariums in November 1950 and May 1951. Additional data were collected from sea lampreys captured in Lake Huron and held in aquariums for

7 months, and on CL–10 which spent more than 2 years of parasitic life in the laboratory.

Recording of feeding time and growth rate

Feeding.—The parasitic activities of the experimental lampreys were observed 7 days a week between November 1950 and June 1952. Individual attacks on or detachments from fish were recorded whenever observed. Four or more complete checks were usually made between 0830 and 1630 hours daily. Once or twice a week, checks were made on the aquarium specimens from 1900 to 0700 hours between early November 1951 and late February 1952. An interpolated hour was listed for most lamprey activities which were initiated or terminated between 1631 and 0759 hours.

There were 8,200 attacks on and detachments from fish listed for lampreys of the second experimental series and specimen CL–10. Of the 4,100 attacks, 49 percent were recorded between 0800 and 1630, and 51 percent between 1631 and 0759 (table 5). Of the 4,100 detachments, 45 percent took place between 0800 and 1630 and 55 percent between 1631 and 0759. Two percent of the total activities which occurred between 1631 and 0759 were observed; the hour of 0100 was assigned to the rest. Considering the disproportionate number of hours in the periods 0800–1630 and 1631–0759, the records show that lampreys are more active during the daylight hours. There were 1.6 attacks or detachments per hour between 0800 and 1630 for each 1 per hour between 1631 and 0759.

Table 5.—Number and percentage of sea lamprey attacks and detachments from prey fish which occurred in aquariums during duty and off-duty hours

[Unobserved attachments or detachments were recorded as taking place at 0100]

Time	Attacks		Detachments	
	Number	Percentage	Number	Percentage
0800 to 1630	2,012	49	1,856	45
1631 to 0759	41	1	44	1
0100	2,047	50	2,200	54
Total	4,100	100	4,100	100

Early in the study of sea lampreys in aquariums it became apparent that attachment time was not synonomous with feeding time. Nonfeeding attachments on prey fish were not uncommon. Lampreys often attached themselves to hosts for considerable periods and then shifted to other sites on the same fish before rasping a feeding hole. On occasion, they remained attached to a feeding site after the host fish died. The same types of attachments were also noted on host fishes captured in our trap nets in Lake Huron. It was therefore necessary to examine all attack sites on prey fish in the aquariums to determine whether feeding had taken place, and to record separately the feeding time and the attachment time. Any time spent on a dead host was also noted.

It is assumed that the figures on feeding time are somewhat high. It was impossible to estimate how long a lamprey actually fed on a wound, but the parasite may have been attached to the feeding site a

number of hours before beginning to feed, and it may have stayed on the wound for some time after it completed feeding. In most attachments, however, observations on the parasite and host led us to believe that the feeding process was started almost immediately, and that detachment occurred soon after it was completed, or upon the death of the fish.

The 22 lampreys which survived to the end of the experiment made a total of 1,920 attacks and spent 63,939 hours attached to fish in aquariums. Included are 52,433 hours (82 percent) of feeding time, 9,452 hours (14.8 percent) of nonfeeding time on live hosts, and 2,054 hours (3.2 percent) on dead fish. On the average, each lamprey made 87 attacks and spent 2,383 hours of feeding and 523 hours of nonfeeding attachment. The ratio of feeding to nonfeeding hours was approximately 4.5 to 1.

Growth.—The dates for the periodic checks on growth in the experimental lampreys were selected arbitrarily at about 6 weeks apart. Considerable variation in time between dates resulted from the pressure of other duties and upon the condition of lampreys and water in the aquariums. Measurements on individual specimens were often postponed for 1 or 2 days if they were engaged in feeding on the checking date. Each lamprey was anesthetized in a solution of urethane, measured and weighed, then replaced in an aquarium immediately.

Trends of feeding and growth

The data on the term lampreys were separated into four groups; a May group and a November group, sexes combined; and a male group and a female group, spring and fall groups combined (table 6). We sought to determine whether any significant differences existed among the groups in their trends of feeding and growth. There were 3 males and 3 females in the November group, and 12 males and 4 females in the May group. The small number of lampreys in each category made it difficult to judge the significance of averages and curves derived from their feeding and growth behavior. At any given point in their parasitic phase, the range of lengths and weights varied widely, as they do in wild lampreys in the lakes.

November and May groups.—The 6 lampreys of the November group averaged 5.7 inches (range, 5.5 to 5.9) and 4 grams when first placed in the aquariums. They made 6 attacks and spent a total of 1,381 hours over feeding sites on prey fish between November and May 14, 1951. Their failure to show any appreciable growth before May was perhaps due to the incomplete development of their feeding mechanism at the time of their lakeward migration in the fall and through the winter (Lennon 1954). It is believed that little actual feeding occurred during the hours listed.

During the next 7 months, May through December 1951, the lam-

Table 6.—Average size of the 22 term lampreys at the end of each measuring period

[Data separated by November and May groups, and by sexes of November and May groups combined]

Measuring period	Sexes combined				November and May groups combined				All lampreys	
	November group		May group		All males		All females			
	Length (inches)	Weight (grams)	Length (inches)	Weight (grams)	Length (inches)	Weight (grams)	Length (inches)	Weight (grams)	Length (inches)	Weight (grams)
1950										
Nov. 22	5.7	4.0								
1951										
May 14	5.7	4.7	5.5	3.3	5.5	3.3	5.7	4.4	5.5	3.6
July 2	7.5	13.2	7.1	10.4	7.1	10.6	7.4	12.4	7.2	11.2
Aug. 13	9.9	27.8	9.4	23.8	9.4	24.2	9.8	26.3	9.5	24.9
Sept. 24	13.6	65.0	12.9	57.6	12.9	58.2	13.5	62.7	13.1	59.6
Nov. 5	15.0	85.5	14.1	71.2	14.2	72.9	14.7	79.7	14.4	75.1
Dec. 17	15.3	88.0	14.4	74.7	14.4	74.3	15.1	86.9	14.6	78.3
1952										
Feb. 4	15.2	87.8	14.4	76.0	14.3	76.3	15.1	85.4	14.6	79.2
Mar. 17	15.0	88.0	14.1	72.5	14.1	73.4	14.7	83.9	14.3	76.7
May 20	14.0	69.8	13.2	60.9	13.3	61.5	13.9	67.4	13.5	63.4
June 26	13.0	54.2	12.5	51.4	12.5	51.8	12.9	52.9	12.6	52.1

preys fed actively, and their rate of growth was rapid. The average maximum size for the group on December 17 was 15.3 inches and 88 grams. Thereafter, size changed little until March 17, 1952, although the amount of feeding done had declined sharply. Mean length and weight decreased steadily as the majority of the specimens approached sexual maturity.

A closely parallel growth rate was exhibited by the 16 survivors of the 60 lampreys stocked in aquariums in May 1951. Their mean size was slightly smaller than that of the November lampreys. The average length on May 3 was 5.5 inches (range 4.9 to 6.4 inches) and mean weight was 3.3 grams (range, 2 to 6 grams). They started to feed and grow immediately and reached their average maximum length of 14.5 inches in December and their average maximum weight of 76 grams in February 1952. Their subsequent decline in size was less than that in the November group. The average terminal measurements for the 16 specimens on June 25, after 13 months in aquariums, were 12.5 inches (range, 10.2 to 14.3 inches) and 51.4 grams (range, 32 to 104 grams) in weight. The mean losses in length and weight since February were 1.9 inches and 24.6 grams, respectively. Individual losses ranged from nil to 3.1 inches and nil to 49 grams.

The average lamprey of the November group fed 2,486 hours during its parasitic life as compared with 2,345 hours of feeding by the average specimen of the May group. The difference of 141 hours may explain the greater size attained by the November lampreys. The average maximum length and weight of the November group exceeded that of the May group by 0.9 inch and 12.0 grams; in average terminal size, the advantages held by the November group were 0.5 inch, length, and 2.8 grams, weight.

Males and females.—Records on feeding and growth by sex for the November and May groups combined revealed that the female lampreys made the greater number of attacks, spent more feeding hours on fish, and grew larger than the males (tables 6 and 7; fig. 1). The percentage distribution of feeding activity for each sex by measuring periods showed that the females did proportionately less of their total feeding, and made fewer attacks, than males in early parasitic life between May and September, but fed more actively in each period from September to June (figs. 2 and 3).

The average female made 111 attachments on fish and fed 2,733 hours, whereas the average male made 76 attacks and fed 2,220 hours during its parasitic life. The females also averaged slightly larger than males at each measuring period. Their maximum length and weight exceeded those of the males by 0.7 inch and 10.6 grams and their terminal advantages were 0.4 inch and 1.1 grams. In spite of the limited data (only 7 females and 15 males), it appears that female sea lampreys feed more and grow larger than males. Further support for this view was found in collections of spawning-migrant sea lampreys from Lake Huron made by Applegate and others (1952) in 1947 through 1951, which showed that mature females averaged slightly larger than males.

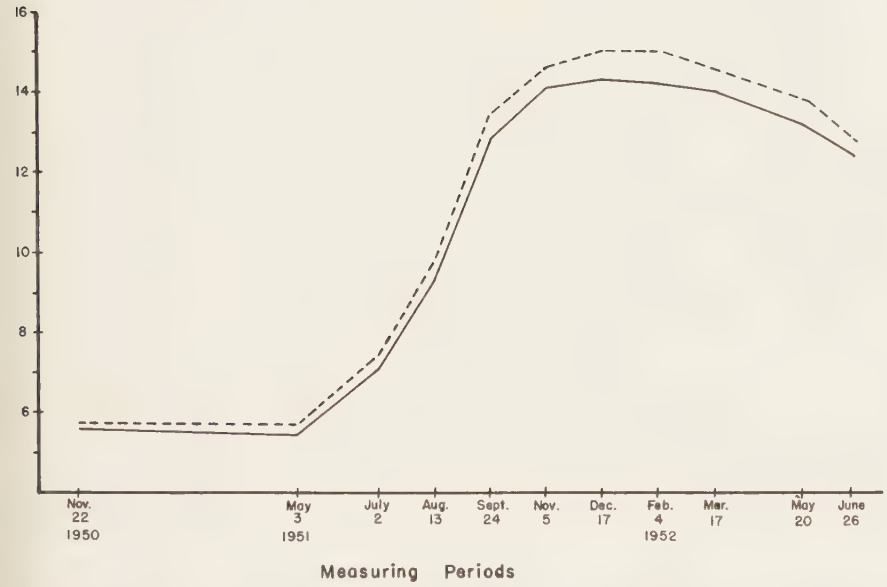
Combined groups.—Little growth was made by fall migrants during their first winter. The same ap-

Table 7.—Percentage distribution of total feeding hours and feeding attacks recorded for 22 sea lampreys which survived to the end of the experiment in aquariums

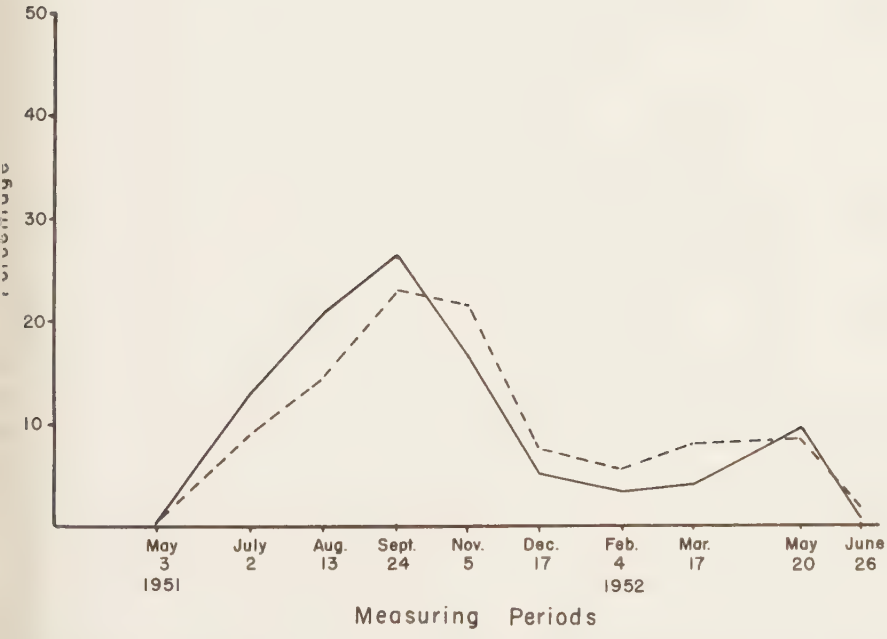
[Data combined for the November and May groups but broken down by sexes for the 15 male and 7 female lampreys]

Feeding period	Male lampreys				Female lampreys				All lampreys			
	Feeding		Attacks		Feeding		Attacks		Feeding		Attacks	
	Hours	Percentage	Number	Percentage	Hours	Percentage	Number	Percentage	Hours	Percentage	Number	Percentage
Nov. 22, 1950 [1] to May 14, 1951	120	0.4	3	0.3	1,261	6.6	3	0.4	1,381	2.6	6	0.
May 3–14 to July 1, 1951	13,895	41.7	150	13.1	5,706	29.8	70	9.0	19,601	37.4	220	11.
July 2 to Aug. 12, 1951	5,279	15.9	238	20.9	2,850	14.9	120	15.4	8,129	15.5	358	18.
Aug. 13 to Sept. 23, 1951	5,505	16.5	305	26.7	3,067	16.0	179	23.0	8,572	16.4	484	25.
Sept. 24 to Nov. 4, 1951	2,809	8.4	190	16.6	1,994	10.4	167	21.5	4,803	9.2	357	18.
Nov. 5 to Dec. 16, 1951	1,492	4.5	56	4.9	1,124	5.9	60	7.7	2,616	5.0	116	6.
Dec. 17, 1951 to Feb. 3, 1952	1,130	3.4	36	3.2	817	4.3	41	5.3	1,947	3.7	77	4.
Feb. 4 to Mar. 16, 1952	933	2.8	46	4.0	759	4.0	63	8.0	1,692	3.2	109	5
Mar. 17 to May 19, 1952	2,004	6.0	112	9.8	1,307	6.8	65	8.4	3,311	6.3	177	9.
May 20 to June 26, 1952	134	0.4	6	0.5	247	1.3	10	1.3	381	0.7	16	0.
Total	33,301	100.0	1,142	100.0	19,132	100.0	778	100.0	52,433	100.0	1,920	100.
Average	2,220		76.1		2,733		111.4		2,383		87.3	

[1] Includes 3 males and 3 females of November group. No growth was made during this period.



gure 1.—Growth curves of male and female lampreys of November and May groups in aquariums. Average lengths plotted by measuring periods between May 1951 and June 1952. Solid line represents 15 males and broken line 7 females.



gure 2.—Percentage distribution of feeding attacks on prey fish by 15 male (solid line) and 7 female (broken line) lampreys, by periods between May 3, 1951, and June 26, 1952.

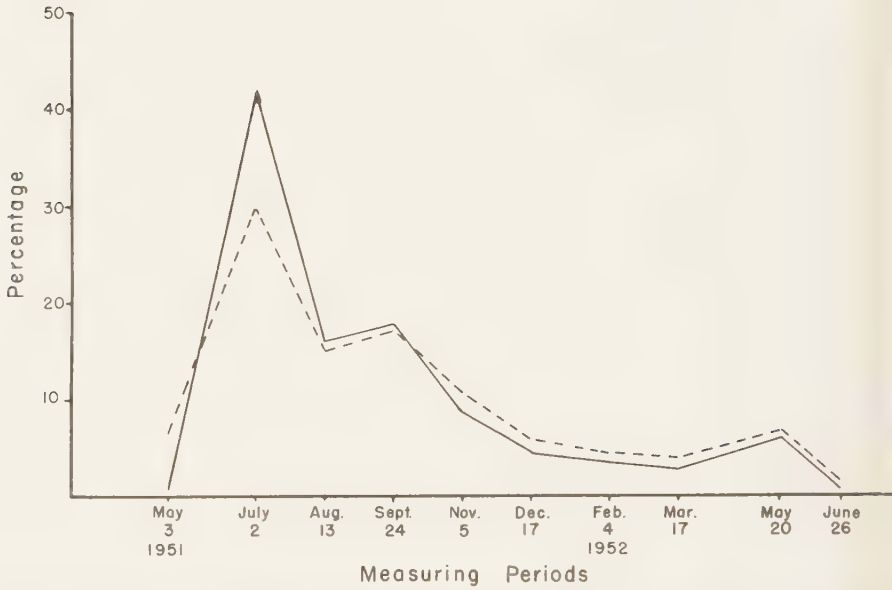


Figure 3.—Percentage distribution of feeding hours recorded for 15 male (solid line) and female (broken line) lampreys, by periods between May 3, 1951, and June 26, 1952.

pears to hold true for fall migrants going into the lake as shown by Lennon's (1954) data on the sizes and seasonal incidence of lamprey wounds on Lake Huron fishes. Between the May 3 and July 2 measuring periods, the fall and spring experimental lampreys began to feed and grow rapidly; 37.4 percent of the total feeding hours and 11.5 percent of the total attacks occurred during this period. On the average, the lampreys fed 134.1 hours to gain 1 gram in weight and spent 87.4 hours of feeding in each attack (table 8). Their mean size at the end of this period was 7.2 inches and 11.2 grams. Feeding efforts in this first period were perhaps less efficient than later, and the percentage of total hours spent was large.

The greatest feeding activity and growth by the term lampreys took

Table 8.—Average number of feeding hou spent per gram of growth gained and p feeding attack by term lampreys in eac measuring period from May 1951 to Jun 1952

Measuring period	Average hours of feeding—	
	Per gram of growth	Per attack on fish
May 10 to July 1, 1951	134.1	87
July 2 to Aug. 12, 1951	29.8	22
Aug. 13 to Sept. 23, 1951	9.1	19
Sept. 24 to Nov. 4, 1951	15.8	14
Nov. 5 to Dec. 16, 1951	45.1	25
Dec. 17, 1951, to Feb. 3, 1952	57.8	30
Feb. 4 to Mar. 16, 1952	(1)	15
Mar. 17 to May 19, 1952	(1)	18
May 20 to June 25, 1952	(1)	23

[1] No gains.

place in the periods between July and November 5, 1951, in spite a 2-week interruption in feeding late July because of an outbreak ichthyophthiriasis. During this in terval, the lampreys doubled the length, spent 41.1 percent of the

total feeding hours, and made 62.4 percent of their total attachments. Maximum feeding occurred between August 13 and September 24. The average gain was 1 gram for 9.1 hours of feeding, and the average duration of attack was 19.4 hours.

The rates of growth and feeding declined after November, but the lampreys reached their average maximum size of 14.6 inches and 78.3 grams between December and February. On February 4, after 9 months of feeding and growth, 89.8 percent of the total hours of feeding and 84.3 percent of the total attacks had taken place. In the remaining 5 months of adult life, the average lamprey shrank in length and weight and, except for a brief period of parasitic activity in the spring, its feeding time and number of attacks continued to decrease.

The reduction of feeding activity was greatest between May 25 and June 25 as most of the term lampreys reached sexual maturity. The efficiency of feeding in the majority of specimens was impaired by the degenerative changes which accompany maturity. The terminal length and weight of the average lamprey were 12.6 inches and 52.1 grams, a decrease of 2.0 inches and 27.1 grams since February.

The experimental lampreys failed to reach as large an average size as members of the same year class in Lake Huron. Data on partial collections made in 1952 indicate that spawning-migrant lampreys from the lake averaged more than 3 inches longer and were approximately twice as heavy as the laboratory specimens. The difference in the terminal sizes of lake and laboratory lampreys might be due to the fact that water temperatures in the aquariums, although within the range of tolerance for lampreys, were higher in summer and lower in winter than subsurface temperatures in the lake. It may be that winter feeding and growth by lampreys continues longer in the lake at 39.2° F. than in the laboratory at about 34° F. Lennon's (1954) data on wounds on lake fish in winter would support this view. Also, the confinement of the specimens to the limited space of aquariums could have had an adverse effect on their growth. Possibly the experimental lampreys failed to compensate for the loss of growth during the 2-week interruption of very active feeding in July 1951 when the outbreak of ichthyophthiriasis occurred.

Immature lampreys.—Two of the 22 term lampreys were considered immature at the conclusion of the experiment, and both had exhibited more feeding activity in the last two measuring periods than the other specimens. Lamprey CL–28, a female of the November group, spent 25 percent of its total feeding time between March 17 and May 14, but shrank from 13.4 inches and 54 grams to 13.1 inches and 47 grams. It did no feeding between May 14 and June 25, and the terminal measurements were 12.5 inches and 40 grams.

A male of the May group, specimen CL–85, did no feeding between December 17 and March 17. Its size was reduced from 11.8 inches and 42 grams to 11.6 inches and 37 grams. Feeding and growth

were resumed in the spring; 9.8 percent of its total attacks on fish and 14.0 percent of its total feeding hours were recorded between March and June. The lamprey completed its last feeding attack on June 13; it was 13.4 inches long and weighed 55 grams when killed and examined on June 25. In view of its immaturity at death and its recent records of feeding, it is possible that CL–85 might have continued to feed and grow for some time.

Specimen CL–10.—Lamprey CL–10 was the only experimental lamprey which lived through 2 years of parasitic life. The specimen was unusual not only in its longevity but also in its feeding and growth (table 9 and fig. 4). It was placed in an aquarium in June 1950, at which time it was approximately 5.5 inches long and weighed about 4 grams. By November it had reached 8.2 inches and 14 grams. From then to May 1951 it did no feeding and shrank 0.1 inch and 4 grams. CL–10 resumed parasitic activity on May 9 and grew steadily until December, when it attained maximum size at 15.4 inches and 75 grams as a result of 32 effective attacks and 1,533 hours of feeding. Again it stopped feeding during the winter and early spring months, but between May 14 and June 26, 1952, it attacked and killed 2 brook trout and 1 white sucker in 165 hours of feeding. CL–10 was 14.0 inches long and weighed 46 grams at this time, when the experiment was terminated.

The two long periods of fast between November and May in 1950–51 and 1951–52 cannot be explained. It may be significant that CL–10 did not feed during the months when water temperatures in the aquarium were generally below 36° F., but other experimental lampreys attacked and fed on prey fish in those months and under the same temperature conditions.

It is noteworthy that lamprey CL–10 shrank during both periods of fast. The reductions were 1.2 percent in length and 28.6 percent in weight between November 1950 and May 1951, and 5.2 percent in length and 32.0 percent in weight between November 1951 and May 1952. The first losses were recuperated during subsequent months of feeding and growth. The reduction in size that started during the second period of fast persisted until specimen CL–10 was

Table 9.—Distribution of attacks on fish, hours of feeding, grams of fish destroyed, and growth exhibited by lamprey CL–10 between June 1950 and June 1952

[Specimen captured as newly transformed adult in Carp Lake River in April 1950]

Measuring period	Number of attacks	Hours of feeding	Fish destroyed (grams)	Size of lamprey	
				Length (inches)	Weight (grams)
1950					
June	0	0	0	[1] 5.5	[1] 4
Nov. 10	[2]	[2]		8.2	14
Dec. 22	0	0	0	8.1	13
1951					
Feb. 2	0	0	0	8.1	12
Mar. 19	0	0	0	8.1	12
May 1	0	0	0	8.1	10
July 2	3	1,023	1,513	10.9	30
Aug. 13	5	166	728	12.4	40
Sept. 24	21	291	2,819	15.1	72
Nov. 5	3	53	496	15.2	78
Dec. 17	2	0	0	15.4	75
1952					
Feb. 4	0	0	0	15.2	71
Mar. 17	0	0	0	14.6	65
May 20	1	24	196	14.6	53
June 26	2	141	134	14.0	46
Total	37	1,698	5,886		

[1] Estimated length and weight at start of parasitic phase.

[2] Number of attacks and hours of feeding between June and November 1950 are unknown.

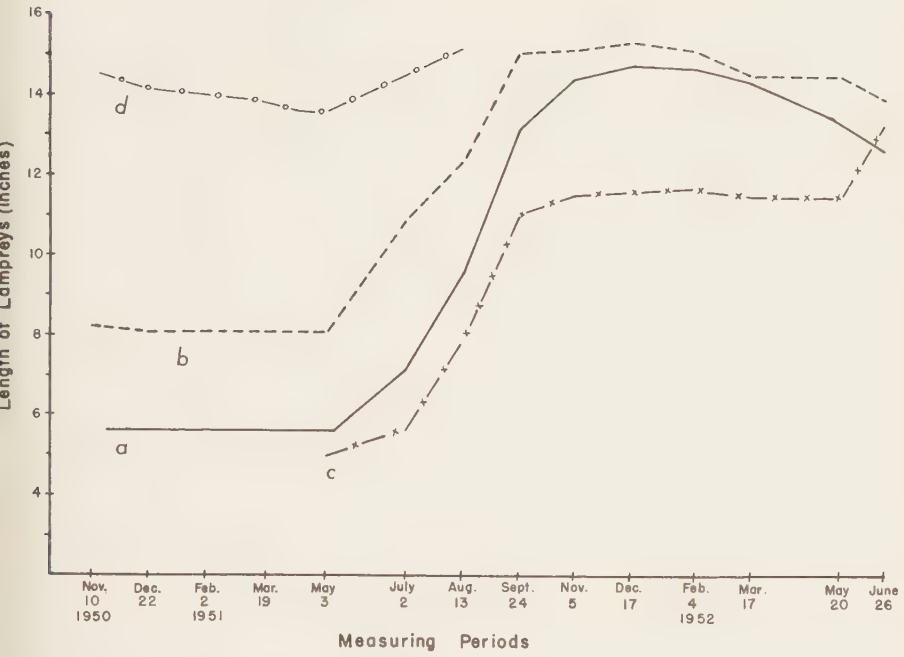


Figure 4.—Growth curves for (a) the average term lamprey (specimen CL–85 excluded), (b) the long-lived specimen CL–10, (c) the immature specimen CL–85, and (d) the lake-captured specimen LH–61. Lengths plotted by measuring periods between November 1950 and June 1952.

killed in late June 1952, although feeding had been resumed in May and continued into June.

Shrinkage.—The shrinkage in term lampreys, in both length and weight, was considerable. The female specimens attained greater maximum size but suffered larger losses than males (fig. 1). In fall and spring lampreys combined, the average loss in length amounted to 23.4 percent of the total gained during parasitic life in females and 11.3 percent in males; the corresponding weight losses were 41.2 percent in females and 33.5 percent in males.

There is also some evidence that the size of wild sea lampreys may decrease as they approach maturity. A decrease was measured in a group of 20 adult lampreys which were captured in trap nets in Lake Huron in the fall of 1950 and placed in laboratory aquariums on November 10. Their average size on this date was 15.8 inches and 104.6 grams. Although all but 3 of the specimens fed on prey fish in the aquariums, these initial measurements were the maximums obtained during their captive life. Of the 16 survivors, 15 were killed in late June 1951; the other was feeding and was spared. The 15 specimens were sexually mature and had decreased on the average 1.9 inches and 36.8 grams. We assumed that

the decreases resulted from natural causes rather than conditions in the aquariums.

The remaining specimen of the lake group, LH–61, demonstrated shrinkage followed by a resumption of growth (fig. 4). It was 14.5 inches long and weighed 63 grams when placed in the tank in November. No feeding was done before May 3, 1951, when it measured 13.6 inches and weighed 42 grams. On May 5, lamprey LH–61 commenced feeding; it made 9 attacks in May and June and fed 765 hours. Its last attack was made on August 6–7 for 11 hours of feeding. The specimen then became infected heavily with fungus and died on August 13. The final measurements were 15.2 inches and 66 grams, which represent increases of 0.7 inch and 3 grams over the measurements recorded in November, and 1.6 inches and 24 grams over the minimums recorded in May.

The observations among experimental lampreys indicate that prolonged periods of abstinence from feeding are accompanied by shrinkage. The losses in length and weight may be overcome if feeding is resumed, as demonstrated by CL–10, CL–85, and LH–61. In general, as lampreys become sexually mature, their feeding activity declines or ceases, and length and weight are reduced. The resumption of feeding by fully mature lampreys is made impossible by the irreversible degeneration of the feeding mechanism and intestinal tract.

Comparison of growth in the laboratory and in the lake.—The pattern of growth of sea lampreys in the Great Lakes is believed to be essentially similar to that observed in aquariums. Applegate's (1950) collections of parasitic lampreys in Lake Huron in 1947–49 indicated that immature lampreys in those years were approximately 8 inches long in June, 16 inches in October and slightly more than 17 inches in December. He had no data on midwinter and early spring lengths.

Lennon (1954) observed that a direct relation exists between the length of lampreys and the sizes of wounds they make on host fish. He found also that the mean diameters of lamprey wounds on fish in Lake Huron were doubled between April and October. The maximum diameters were measured in February; thereafter, as the lampreys approached maturity, the mean diameters of the wounds decreased. These data on wound sizes and lampreys in Lake Huron compare well with the pattern of growth observed in experimental lampreys in aquariums.

RELATION BETWEEN LAMPREY FEEDING AND FISH MORTALITY

The study of sea lampreys in aquariums afforded an opportunity to determine the quantity of prey fish required by a parasitic-phase lamprey to grow from metamorphosis to sexual maturity. Thereby, an estimate could also be made on the destruction of fish by individual lampreys in the Great Lakes.

The methods of recording the attacks and feeding hours of the experimental lampreys and information on the host fish have already been described. The computation from the records of food consumption and fish-kill was complicated by the frequent incidence of multiple attacks on individual fish. It was frequently impossible to determine which lamprey fed more effectively, or contributed most towards the death of the host.

To obtain estimates of food consumed by individual lampreys, the feeding data and the amount of fish killed were totaled for each aquarium by measuring periods. The kill of fish was then prorated among the lampreys according to their individual gains in growth. For example, during a certain period of approximately 6 weeks 6 lampreys were present in aquarium 6. They made 116 attacks on fish, fed 2,073 hours, and gained totals of 19.6 inches in length and 190 grams in weight. Forty fish which weighed a total of 15,506 grams were destroyed as a result of the attacks. From such data, the number of hours of feeding and the number of grams of fish killed for each gram of weight gained by an experimental lamprey were computed. Once these values were obtained, it was possible to determine the number of grams of fish killed by term lampreys, since their feeding hours and gains in weight were known.

The records collected for each aquarium in each period necessarily included feeding time and attacks made by lampreys which died before the experiment was terminated. Inspection of the data showed that their feeding and growth were not significantly different in any period from those of the full-term lampreys.

The November 1950 and May 1951 groups of lampreys were maintained separately among the 11 aquariums. The records obtained for either group distributed among several aquariums were combined, since no differences were found in the patterns of feeding and growth between occupants of individual aquariums. There were some differences, however, between the November and May groups and between males and females of both groups, but as expected, the variations within a group in feeding, growth, and fish-kill exceeded the discrepancies between means of different groups. This may also be true for sea lampreys of any year class in the lakes, since its individuals vary widely in length and weight at any given time.

Destruction of fish

November and May lampreys.— The 22 term lampreys destroyed 408 pounds of fish in 1,920 attacks and 52,433 hours of feeding during their parasitic phase of life (table 7). The white sucker, principal prey species in the experiment, comprised 86.9 percent of the total weight of fish killed (table 10). Rainbow trout constituted 9.9 percent of the total weight destroyed, brook trout 1.3 percent, and other species combined amounted to 1.9 percent.

Among the 6 term lampreys of the November group, the average specimen killed 9,806.7 grams (21.6 pounds) of fish in its 18 months of adult life (table 11). The difference between its initial and terminal

Table 10.—Species, number, average size, and total weight of fish killed outright by all expe mental sea lampreys in aquariums between November 22, 1950, and June 25, 1952

Species	Number of fish	Length		Weight		Total weight	
		Average (inches)	Range (inches)	Average (grams)	Range (grams)	Pounds	Percen age
Brown trout	17	10.2	7.9–12.4	165	80–260	6.2	
Rainbow trout	293	9.6	6.8–13.0	129	53–354	83.7	
Brook trout	45	8.6	5.1–11.5	109	16–228	10.8	
Lake trout	1	8.0		60		0.1	
White sucker	903	12.5	6.5–16.5	369	36–870	734.3	8
Longnose sucker	9	12.8	9.2–16.2	420	128–830	8.3	
Yellow perch	5	8.9	7.9–10.3	133	80–224	1.5	
Total	1,273					844.9	10

Table 11.—Total weight of fish destroyed and fish-kill per gram of growth by the average la prey of the November group and of the May group, sexes combined, and by the avera male and the average female of the fall and spring groups combined

Average lamprey of group—	Total number of fish killed		Fish-kill per gram of growth at—			
			Maximum size		Terminal size	
	Grams	Pounds	Growth (grams)	Fish-kill (grams)	Growth (grams)	Fish-ki (grams
November 1950	9,806.7	21.6	84.0	95.4	50.2	19
May 1951	7,893.5	17.4	72.7	92.7	48.1	16
Males	7,537.8	16.6	73.0	88.0	48.5	15
Females	10,295.5	22.7	82.5	103.1	49.1	20

weights was 50.2 grams; thus each gram represented 195.3 grams of fish destroyed. The average lamprey actually gained 84 grams to reach its maximum weight, at a ratio of 1 gram of growth for 95.4 grams of fish killed. The subsequent shrinkage in length and weight took place in spite of some feeding.

The average lamprey of the 16 May specimens destroyed 7,893.5 grams (17.4 pounds) of fish in its 14 months of parasitic life at a ratio of 164.1 grams of prey for each gram of the 48.1 grams difference between initial adult and terminal weights. The maximum weight gained by the lamprey was 72.7 grams at a ratio of 1 gram of growth for 92.7 grams of fish killed.

The destruction of fish by th average November lamprey ex ceeded that of the average Ma specimen by 4.2 pounds. Th November lamprey also fed greater number of hours and ha slightly greater initial, maximum and terminal sizes than the Ma parasite. However, the ratios weight gain in lampreys of bot groups to weight of fish killed fo the period between initial an maximum size differed by only 2 grams.

Male and female lampreys.—Th average female lamprey made mo attacks on fish, did more feedin and surpassed the average ma by 0.7 inch in length and 10 grams in weight, at maximum siz and by 0.4 inch and 1.1 grams

erminal size. She destroyed 0,295.5 grams (22.7 pounds) of sh (table 11) during parasitic life s compared with 7,537.8 grams 16.6 pounds) killed by the average ıale. For each gram gained to ɔach maximum size, the female estroyed 103.1 grams of fish and ıe male 88.0 grams. At terminal .ze, the female had killed 209.7 rams and the male 155.4 grams f fish for each gram of growth over ıeir initial weights.

The ratios of lamprey growth to sh-kill to reach maximum size ıggest that the males utilized their ɔod to better advantage than the ɛmales. The greater difference in he ratios at terminal size was due artly to the fact that females did ıore feeding in the latter part of arasitic life than males, yet shrank ıore in length and weight.

ize relations

The size of the lampreys was orrelated with their efficiency in feeding and their destruction of fish. When the lampreys were small and their first attacks relatively inefficient, they fed, on the average, 14.9 hours per day between May 3 and July 2, but only 0.3 gram of fish was killed per hour (table 12). As they grew, the daily rate of feeding diminished, but the destruction of fish increased sharply, and the average maximum rate was 8.5 grams of fish an hour between September 24 and November 5. Feeding, growth and fish-kill tapered off quickly after December 17. In the period between March 17 and May 20, the losses in length and weight were rapid in spite of a brief increase in feeding activity when, on the average, lampreys fed 2.4 hours a day and 5.8 grams of fish were destroyed per hour. The feeding efficiency of some specimens may have been impaired at this time by degeneration of the feeding mechanism and the approach of sexual maturity.

able 12.—Average number of feeding hours, fish-kill per hour of feeding, and total weight of fish destroyed by the 22 term lampreys between May 1951 and June 1952

[Data arranged by measuring periods; dates are inclusive]

Measuring period	Size of lamprey		Number of feeding hours—		Fish killed per feeding hour (grams)	Total number of fish killed	
	Length (inches)	Weight (grams)	Per period	Per day		Grams	Pounds
ay 3 to July 1	6.4	7.6	891.0	14.9	0.3	276.2	0.6
ly 2 to Aug. 12	8.4	18.2	[1] 369.5	8.8	2.9	1,070.7	2.4
ug. 13 to Sept. 23	11.3	42.3	389.6	9.3	8.0	3,116.8	6.9
pt. 24 to Nov. 4	13.8	67.4	218.3	5.2	8.5	1,855.5	4.1
ov. 5 to Dec. 16	14.5	76.7	118.9	2.8	3.5	416.2	0.9
ec. 17 to Feb. 3	14.6	78.8	88.5	1.8	3.7	326.6	0.7
eb. 4 to Mar. 16	14.5	78.0	76.9	1.8	4.9	376.8	0.8
ar. 17 to May 19	13.9	70.1	150.5	2.4	5.8	866.9	1.9
ay 20 to June 26	13.1	57.8	17.3	0.5	6.9	119.4	0.3
All periods			2,320.5	5.5	3.6	8,425.1	18.6

[1] Feeding was interrupted for 2 weeks from July 21 to August 1 while an infection of ichthyophthiriasis was eated. Hence, the number of feeding hours may have been greater for this period.

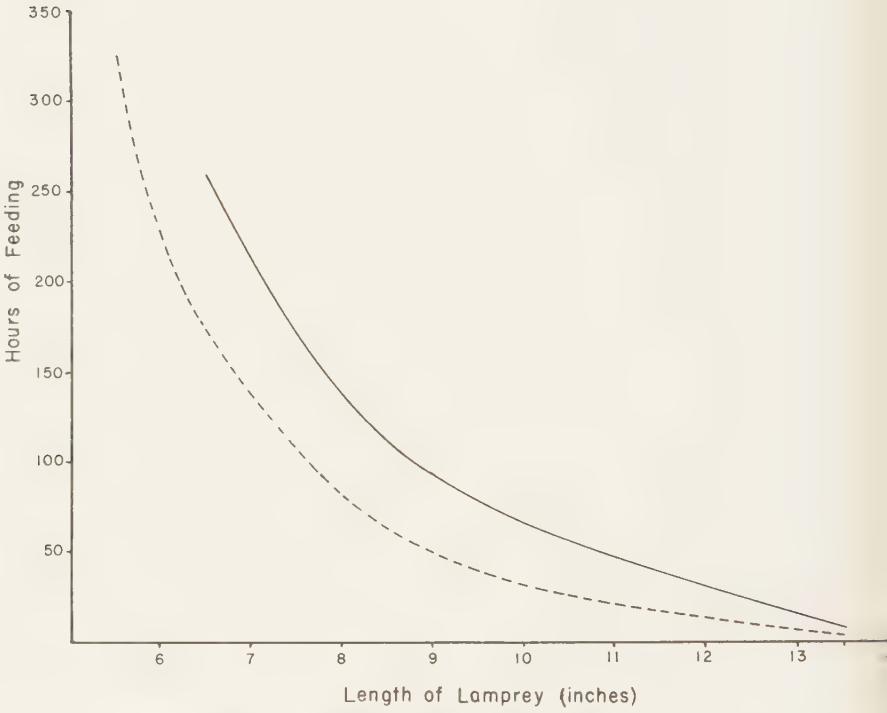


Figure 5.—Relation of length of lamprey to hours of feeding required to kill white suckers (soli line) 12.0 to 12.9 inches long and rainbow trout (broken line) 9.0 to 9.9 inches long. Th average lengths of lampreys and their hours of feeding were computed from data collecte on all experimental specimens between May 3 and November 5, 1951.

The increase in destructiveness of growing lampreys was exhibited by plotting the hours of feeding by various sizes of parasites which resulted in the deaths of host fish of certain sizes (table 13 and fig. 5). Averages indicate that a 6.2-inch lamprey killed white suckers of 12.0 to 12.9 inches long in 344.5 hours of feeding. In contrast, a 13.0-inch lamprey destroyed suckers of the same size range in 39.3 hours. For rainbow trout between 9.0 and 9.9 inches long, the 6.2-inch lamprey fed 244.5 hours to kill, and the 13.0-inch parasite 19.1 hours.

As expected, small fish succumbed more quickly than large hosts from attack by lampreys of a certain size range (table 14 and fig. 6). During

Table 13.—Mean number of feeding hours b lampreys of various sizes which resulted i deaths of white suckers 12.0 to 12.9 inche long, and rainbow trout 9.0 to 9.9 inche long

[Average lengths of lampreys and their feeding hou computed from data collected on all experiment specimens between May 3 and November 5]

Length of lamprey	Hours of feeding	
	White suckers	Rainbo trout
6.2 inches	344.5	244
8.2 inches	86.9	42
10.8 inches	46.2	21
13.0 inches	39.3	19

the period August 13–November 5 when the experimental lamprey were attacking most effectively white suckers between 9.0 and 9. inches long were killed after an ave age of 18.8 hours of feeding, where

Table 14.—Mean number of feeding hours which resulted in death of white suckers of certain size groups during period August 13 to November 5 when the experimental lampreys averaged 12.6 inches long

Length group of fish	Number of fish	Average number of feeding hours
9.0 to 9.9 inches	14	18.8
10.0 to 10.9 inches	36	30.9
11.0 to 11.9 inches	56	33.9
12.0 to 12.9 inches	132	42.9
13.0 to 13.9 inches	163	54.0
14.0 to 14.9 inches	71	55.9

more than twice as many hours were required to kill hosts between 12.0 and 12.9 inches long. For suckers of 14.0 to 14.9 inches, an average of 55.9 hours of feeding by lampreys produced death.

The ability to survive attack by lampreys of certain size may be no greater in the larger host fish, but time confers an advantage on them. The rate of food intake by a given lamprey is nearly constant on large or small hosts, but the demand made on a small fish may exceed its capacity to compensate losses. The larger fish supplies more food and consequently has more time for hemopoiesis and other physiological functions to correct the imbalance in blood supply, water, and tissue relations caused by lamprey feeding (Lennon 1954). If the parasite becomes satiated and terminates the attack before it can overcome the normal and compensatory limits of the host, the fish may survive.

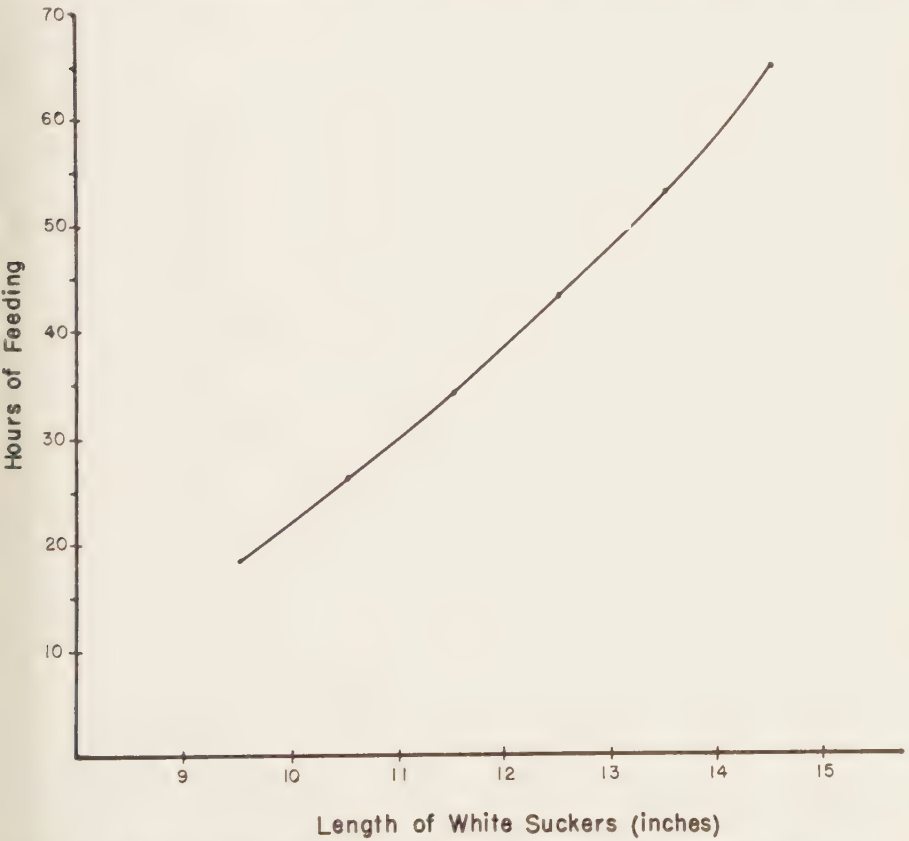


Figure 6.—Relation of hours of feeding by an average 12.6-inch lamprey to lengths of white suckers which died under attacks in the period August 13 to November 5, 1951.

In general, it appeared that larger fish had greater opportunity than small hosts for living through a lamprey attack and possible secondary effects thereof.

Since the size of lampreys is correlated with their destructiveness to host fish, it appears that the average fish-kill per lamprey in the lakes may be substantially greater than that observed in the laboratory. The mean terminal size of the 22 experimental lampreys was 12.6 inches and 52.1 grams; the average fish-kill during their parasitic phase was 18.5 pounds. In contrast, the mean size of spawning migrant lampreys of the same year class in Lake Huron was approximately 16.0 inches and 125 grams. On the basis of length and weight differences between laboratory and lake lampreys, and with reference to the ratios of fish destruction per gram of growth expressed previously for male and female experimental specimens, we estimate that the average fish-kill by wild lampreys exceeds, and could be approximately double, the 18.5 pounds recorded for laboratory lampreys. Further refinement of this estimate was not attempted, since the failure of the experimental lampreys to reach larger size could not be resolved.

Incidence of attacks on fish

Multiple attacks.—Attacks by two or more lampreys on individual host fish have been observed in the lakes and in aquariums. Royce (1950) noted multiple scars made by lampreys on lake trout in Seneca Lake. Hall and Elliott (1954) found as many as 5 scars on single white suckers in Lake Huron, and they showed that the incidence of multiple scarring tended to increase with increase in length of the fish.

Many of the fish used in the aquariums incurred multiple attacks. Of the 903 white suckers and 293 rainbow trout killed outright during the experiment, 82.4 percent of the suckers and 60.8 percent of the rainbow trout were attacked by two or more lampreys. No pattern could be defined for these multiple attachments other than that the incidence differed among fish of various sizes. Small hosts incurred fewer attacks than large ones, partly because they succumbed relatively soon and partly because they attracted fewer.

Lennon (1954) reported that a fish struggling to dislodge a lamprey frequently draws other attackers to itself. In many such cases, however, one or more of the several lampreys that may attach themselves to the prey fish do no feeding.

An analysis of data on multiple attacks was complicated by the fact that some attachments occurred separately and others simultaneously. When a prey fish died as a result of two or more attacks, assessment of the amount of individual feeding and contribution to the death was difficult. The sizes of lampreys attacking a given fish usually varied, as did the duration of the attachments, and perhaps the intensity of their attacks. Furthermore, one of the lampreys might press its attack on a more rewarding site on the fish, another on a more damaging site, and others on relatively less effective sites. Other considerations include the individual differences in feeding

by lampreys of the same size, by lampreys of different sizes, and by lampreys of different degrees of maturity.

The least complicated body of data on the incidence and effects of multiple attacks was obtained from white suckers and rainbow trout killed by lampreys in the experimental series between August 13 and November 5. During this period, most of the multiple attacks occurred simultaneously, that is, two or more lampreys were often found on a fish at the same time, although their attachment and detachment times might differ considerably. At this time, also, single or multiple attacks were particularly lethal and most host fish lived only a few days in the aquariums.

During the 12-week period, 472 white suckers were killed by the experimental lampreys, of which 135 (28.6 percent) suffered single attacks (table 15). There were 192 suckers (40.6 percent) destroyed with 2 attacks, but only 1.7 percent were subject to 5 or more attacks. The majority of small suckers, between 100 and 299 grams, died after 1 or 2 attacks, whereas only the largest fish, betweeen 400 and 599 grams, incurred as many as 5 to 8 attacks.

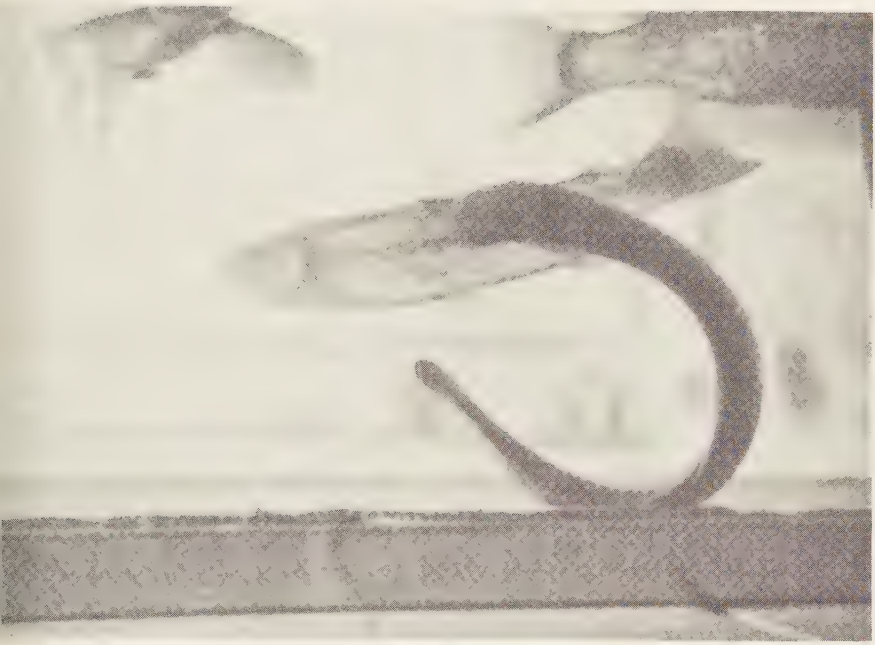
A comparison of the data on fish killed by 1 or more lampreys revealed that, in general, considerably more feeding time was spent on multiple attachments than in single attacks. A white sucker weighing between 300 and 399 grams died on the average after 26.1 hours of feeding by a single lamprey. When 2, 3, or 4 attacks were made on individual fish of the same size, the total hours of feeding before death were 43.6, 56.5, and 56.3, respectively. Among the larger suckers, of 400 to 499 grams, death resulted from 1 attack after 31.7 hours of feeding, from 2 attacks after 50.6 hours, 3 after 78.7 hours, 4 after 75.3 hours, 5 after 89.5 hours, 6 after 104.5 hours, and 8 after 82 hours. As the number of lampreys attached to a fish increased, however, the average number of hours of feeding per attacker tended to decrease. A single lamprey spent 26.1 hours on a sucker weighing 300 to 399 grams, whereas the average attack by 2 lampreys lasted 21.8 hours, by 3 lampreys 18.8 hours, and by 4 lampreys 14.1 hours.

Of the 74 rainbow trout killed by lampreys between August 13 and November 5, 55 (74.3 percent) sustained single attacks and 19 (25.7 percent) suffered 2 attacks (table 16). The rainbow trout averaged nearly 2 inches shorter and 240 grams lighter than the white suckers, and they died sooner under attack than the larger suckers. Consequently, the rainbow trout attracted fewer multiple attachments because of their size, or failed to live long enough under 1 or 2 attacks to incur additional ones. The limited data on rainbow trout agreed with those on white suckers with respect to total hours of feeding. The number of feeding hours to cause death increased in multiple attacks. The average rainbow trout between 100 and 199 grams died after 17.9 hours of feeding by a single lamprey, and after 34.8 hours by 2 lampreys.

Table 15.—Average number of feeding hours spent by lampreys per attack and per fish to kill white suckers of certain weight groups in single and multiple attacks

[Data collected between August 13 and November 5, 1951, when the experimental sea lampreys averaged 13.1 inches long and 59.6 grams in weight]

Weight group of fish	Fish killed		Total hours of feeding	Average hours of feeding	
	Number	Percentage		Per attack	Per fish
1 attack:					
100–199 grams	14		255	18.2	18.2
200–299 grams	25		369	14.8	14.8
300–399 grams	38		993	26.1	26.1
400–499 grams	50		1,584	31.7	31.7
500–599 grams	8		334	41.7	41.7
Total	135	28.6			
2 attacks:					
100–199 grams	8		220	13.7	27.5
200–299 grams	37		1,359	18.3	36.7
300–399 grams	59		2,571	21.8	43.6
400–499 grams	56		2,832	25.3	50.6
500–599 grams	30		1,456	24.2	48.5
600–699 grams	2		72	18.0	36.0
Total	192	40.6			
3 attacks:					
100–199 grams	2		79	13.3	39.5
200–299 grams	11		624	18.9	56.7
300–399 grams	38		2,147	18.8	56.5
400–499 grams	38		2,991	26.2	78.7
500–599 grams	12		744	20.7	62.0
600–699 grams	1		69	23.0	69.0
Total	102	21.6			
attacks:					
100–199 grams	1		162	40.5	162.0
200–299 grams	3		259	21.6	86.3
300–399 grams	14		788	14.1	56.3
400–499 grams	13		979	18.8	75.3
500–599 grams	4		350	21.9	87.5
Total	35	7.4			
5 attacks:					
100–299 grams					
300–399 grams	1		132	26.4	132.0
400–499 grams	2		179	17.9	89.5
500–599 grams	1		107	21.4	107.0
Total	4	0.9			
6 attacks:					
100–399 grams					
400–499 grams	2		209	17.4	104.5
Total	2	0.5			
7 attacks:					
100–499 grams					
500–599 grams	1		116	16.6	116.0
Total	1	0.2			
8 attacks:					
100–399 grams					
400–499 grams	1		82	10.3	82.0
Total	1	0.2			
Grand total	472	100.0			



ure 7.—Brown trout, approximately 12 inches long, under attack by an experimental sea lamprey in an aquarium at Hammond Bay Fishery Laboratory.

ble 16.—Average number of feeding hours spent by experimental lampreys per attack and per fish to kill rainbow trout of certain weight groups in single and multiple attacks

Data collected between August 13 and November 5, 1951, when the lampreys averaged 13.1 inches long and 59.6 grams in weight]

Weight group of fish	Fish killed		Total hours of feeding	Average hours of feeding	
	Number	Percentage		Per attack	Per fish
Attack:					
100–99 grams	21		284	13.5	13.5
100–199 grams	32		574	17.9	17.9
200–299 grams	2		137	68.8	68.8
Total	55	74.3			
Attacks:					
100–99 grams	7		172	12.3	24.6
100–199 grams	11		383	17.4	34.8
200–299 grams					
300–399 grams	1		47	23.5	47.0
Total	19	25.7			
Grand total	74	100.0			

We can offer no explanation for greater numbers of feeding urs recorded in the multiple acks. The blood and body ces of a fish are limited in quantity, and death occurs as these fluids approach exhaustion in single or multiple attacks by lampreys. Since the number of hours of feeding to cause death was con-

siderably larger in multiple than in single attacks, each participating lamprey must obtain, in addition to flesh, a small yet sufficient fraction of the fluid to induce it to remain on the host. Usually, as soon as a lamprey receives too little return for its feeding effort, or the fish dies, it detaches and seeks a new host (Bigelow and Welsh, 1925).

Single attacks.—Lennon (1954) discussed the distribution of sea lamprey wounds on the bodies of host fish in the lake and in aquariums, using combined data on single and multiple attacks. We found no significant differences when the wound distribution plotted by us on combined attacks by one or more lampreys was compared with the pattern described by him. However, no presentations have been made previously on the distribution of single attacks alone on host fish. All wounds on white suckers and rainbow trout killed in one attack by lampreys of the November and May groups were located according to body regions on the prey fish. The data on the attacks were further treated separately by periods between Ma 1951 and June 1952 (table 17).

Single attacks by lampreys caus the destruction of 159 white sucker or 17.6 percent of the 903 specime of this species killed outright duri the experiment. An inspection these hosts showed that an atta by one lamprey on any part of fish's body, exclusive of fins, can l lethal. Most of the single attac were on the head and on t dorsal surfaces of the midportion the body, above the lateral lin Considering the disproportiona surface areas in the body regio listed (16 percent of the total bo area in region I, 30 percent in I 35 percent in III, and 19 percent IV), it is apparent that for a giv unit of surface area the he received the greatest number attacks.

The separation of the data periods indicates that an attack a single lamprey in any stage of parasitic life between metamo phosis and maturity can be dead to the host fish. Most of the sing attacks were recorded betwe August 13 and November 5, 19

Table 17.—Distribution of single attacks by experimental lampreys that caused the deaths 159 white suckers and 115 rainbow trout, by periods between May 1951 and J 1952

[Body regions defined on the fish were: I, entire head (16 percent of total surface area on both species); II, surface of midportion of body above lateral line and between head and anus (30 percent); III, all surface of portion of body below lateral line between head and anus (35 percent); and IV, all surface of body betw anus and caudal fin (19 percent). Area percentages taken from Lennon (1954).]

Period	Numbers of single attacks in—							
	Region I		Region II		Region III		Region IV	
	Sucker	Trout	Sucker	Trout	Sucker	Trout	Sucker	Tro
May 3 to Aug. 12, 1951	4	1	2	37		17		
Aug. 13 to Nov. 4, 1951	41	2	63	43	27	10	1	
Nov. 5 1951, to Feb. 3, 1952	4		7	1	2	1		
Feb. 4 to June 25, 1952	5		1		2			
Total	54	3	73	81	31	28	1	

ıen the lampreys were feeding th greatest effectiveness, growing pidly, and killing the most fish. Single attacks resulted in the ath of 115, or 39.2 percent of the 3 rainbow trout killed by the perimental lampreys. Whereas e percentage distribution of body rface among the regions listed was proximately the same as for the ıite suckers, relatively few attacks curred on the heads of trout. ost of them were above the lateral ıes on the midportion of the body tween the head and anus, but hal attacks did take place on all gions from head to tail.

The distribution of single attacks these white suckers and rainbow ɔut conformed to the patterns scribed by Lennon (1954). We ncur that no explanation can be ven for the apparent preference by mpreys for attacking the heads of ıite suckers and their avoidance this region on rainbow trout, and eir avoidance of the peduncular gion in both species.

It proved impractical to analyze e hours of feeding spent in single tacks on white suckers and rain-ɔw trout according to body regions ıd by periods. Since the numbers hours of feeding to produce death ıried widely according to the size the lampreys and of the host fish, ıd by periods, the averages com-ıted for the few attacks listed for me body regions were entirely unreliable. Single attacks on white suckers lasted from 2 to 362 hours and on rainbow trout from 2 to 72 hours. In general, wounds on the heads of both species were more quickly lethal than elsewhere on the body.

Survival of host fish

A total of 54 fish (4 percent of all host fish) survived attacks by the lampreys in the aquariums. They included 21 white suckers between 9.2 and 15 inches long and 12 rainbow and brown trout between 9 and 12.4 inches long, which died soon after from fungus infections in their wounds or from high turbidity in the water. The specimens were so weakened by the lampreys that their recovery in the lake or laboratory would have been very doubtful.

Temporary difficulties with the water supply in July 1951 forced us to interrupt the feeding on 21 fish (1.6 percent of the host fish used) by experimental lampreys which averaged about 8 inches long. Fourteen white suckers were released in the lake, but 7 rainbow trout between 8.5 and 11.2 inches long were transferred to a livecar in the lake. Although the durations of attacks on these trout ranged from 5 to 39 hours, they did not appear to be greatly weakened. In spite of only occasional feeding with a hatchery diet, the trout recovered, and their wounds healed completely within 2 months.

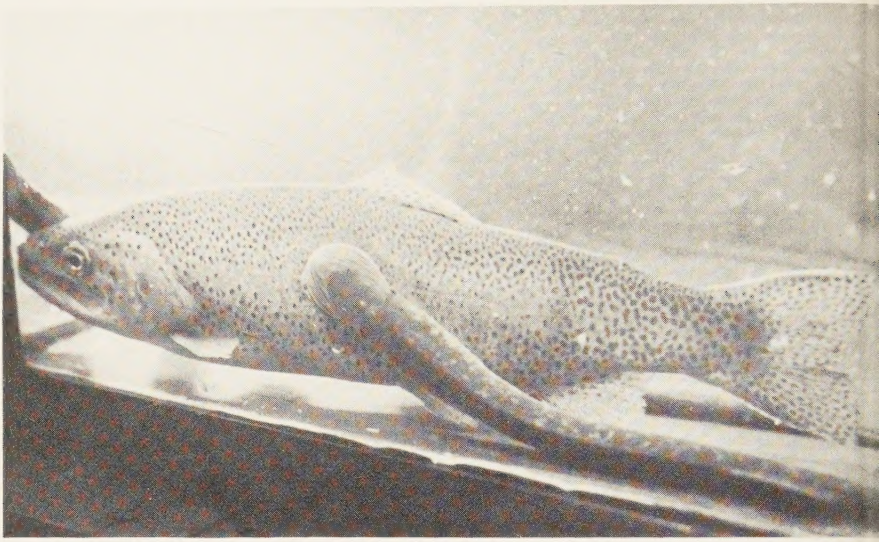


Figure 8.—Rainbow trout, 15.0 inches long and 622 grams in weight, attacked and killed b experimental sea lampreys in an aquarium on May 14–15, 1951. Lamprey LH–7 15.3 inches long, fed on right side of host for 6 hours; lamprey LH–65, 16.5 inches lo fed on left side for 14 hours.

SUMMARY

The investigations on sea lampreys in aquariums were concerned with the duration of the parasitic phase, feeding and growth, and the interrelations between predator and host fish.

Most of the experimental lampreys were mature and ripe after 14 to 18 months of parasitic life. They exhibited secondary sex characters and the signs of irreversible physical degeneration which attend spawning and imminent death. Records on 3 specimens that were immature after 14, 18, and 26 months in aquariums indicate that under certain, perhaps adverse, conditions a lamprey can extend its parasitic phase of life before reaching maturity.

The newly transformed sea lampreys placed in aquariums, including both fall and spring downstrea migrants, averaged 5.5 inches an 3.6 grams when active feeding an growth commenced in late spring The greatest feeding activity an growth occurred from midsumme through early fall. There was sharp decline in activity durin winter, and the lampreys reache the maximum average size of 14. inches and 78.3 grams. Thereafte and throughout the spring th specimens shrank in length an weight. Their average termin size was 12.6 inches and 52.1 gram

On the average, a lamprey in th experimental series engaged in 2,38 hours of feeding and killed 18 pounds of fish in 87.3 attacks durin its parasitic life. Female lampre made more attacks, fed more, kille more fish, and grew larger tha

males. They also shrank proportionately more in length and weight as they approached sexual maturity, but their average terminal size was slightly greater than that of males.

The parasitic activity, growth, and shrinkage observed among the lampreys in the experimental series were considered to be typical of sea lampreys in the lakes. On the basis of length and weight differences between laboratory and lake lampreys, and with reference to the ratios of fish destruction per gram of growth expressed for male and female experimental specimens, it is estimated that the average fish-kill by a wild lamprey exceeds, and could be approximately double, the 18.5 pounds of fish killed by a lamprey in the laboratory aquariums.

The interrelation between the parasites and their hosts showed that the rate and extent of fish destruction depended on the size, sex, and stage in the parasitic phase of the lampreys, and on the species and size of the fish. There was an increase in the number of fish killed as the lampreys grew, and the fish were killed more quickly. Small fish succumbed sooner than large ones as a result of attacks by lampreys of a certain size range.

Many of the fish in aquariums were attacked by two or more lampreys, either separately or simultaneously, but small hosts incurred fewer multiple attacks than large ones. In general, the total number of feeding hours recorded in multiple attacks was greater than in single attacks. As the number of lampreys feeding on a fish increased, however, the average number of feeding hours per attacker tended to decrease. Inspection of single wounds on white suckers and rainbow trout showed that attacks made by experimental lampreys at any stage of their parasitic phase of life up to full maturity, and on any part of a prey fish, except fins, may be lethal.

Of the small number of white suckers and rainbow trout which survived attacks by lampreys in the laboratory experiments, most died soon after from infections by fungi in their wounds or from turbid water conditions. Among the remainder were 7 rainbow trout which survived attacks of 5 to 39 hours duration. These 7 fish recovered, and their wounds healed completely.

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